THE NEUROSECRETORY SYSTEM OF BRACHYURAN CRUSTACEA [1, 2]

DOROTHY E. BLISS AND JOHN H. WELSH

The Biological Laboratories, Harvard University, Cambridge 38, Massachusetts

Physiological evidence has accumulated which no longer favors the sinus gland as the site of formation of the molt-inhibiting hormone of Crustacea (Bliss, 1951, 1952; Frost, Saloum and Kleinholz, 1951; Havel and Kleinholz, 1951; Passano, 1951a, 1951b, 1952a, 1952b; Travis, 1951a, 1951b; Welsh, 1951). The present studies, designed originally to correlate anatomical relationships of the neurosecretory organs in the brachyuran, *Gecarcinus lateralis* (Fréminville), with the molt and respiratory data recorded on this animal (Bliss, 1951, 1952), include comparative observations on a variety of crabs. It has become clear that assignment of crustacean endocrine functions primarily to the so-called sinus glands has been an over-simplification of a very complex situation.

Materials and Techniques

Specimens of *Gecarcinus lateralis* were shipped periodically to Cambridge from Bermuda. Most other crabs included in this paper were studied in Bimini, B. W. I., while the first author was a Guest Investigator at the Lerner Marine Laboratory of the American Museum of Natural History.

The characteristic bluish-white hue of the living sinus gland was first noted by Brown (1940), his diagrams of several decapod eyestalks depicting not only the sinus gland but its large bluish-white nerve as well. Both sinus gland and nerve are visible when eyestalks of *Gecarcinus* are dissected either in sea water or in a suitable perfusion fluid. It is possible, after removal of the connective tissue sheath surrounding the ganglia, to trace numerous bluish-white nerve tracts that converge and enter the sinus gland. An intense spot of light reveals the deeper of these tracts.

Accentuation of nerve tracts and bluish-white globules, which have proved to be groups of neurosecretory cells, occurs in eyestalks and brain when a preparation is permitted to stand for some time in the beam of a microscope lamp. Increase in salt concentration due to evaporation of perfusion medium causes tracts and globules already visible to become whiter and others hitherto unseen to be apparent. This effect is accomplished more rapidly by use of concentrated sea water or hypertonic perfusion fluid. Addition of a drop or two of glycerol, which clears the tissue, further intensifies nerve tracts and globules. Careful dissection exposes these tracts as groups of brilliant white fibers.

[1] This work was supported in part by a research grant from the Division of Research Grants and Fellowships of the National Institutes of Health, U. S. Public Health Service.

[2] A portion of this work was done at the Lerner Marine Laboratory of the American Museum of Natural History, Bimini, B. W. I.

A modification of the conventional methylene blue technique for nerve differentiation has proved useful. The eyestalk ganglia and brain, stripped of their connective tissue sheath, are placed in the well of a depression slide, containing about 20 drops of perfusion medium and two drops of 0.2% methylene blue. After several minutes the preparation is examined against a black background in the same amount of perfusion medium and two drops of glycerol. Alternate staining and clearing yields a preparation in which nerve cells appear deep blue and nerve tracts white with blue edges. Since it is known that both neurosecretory and other

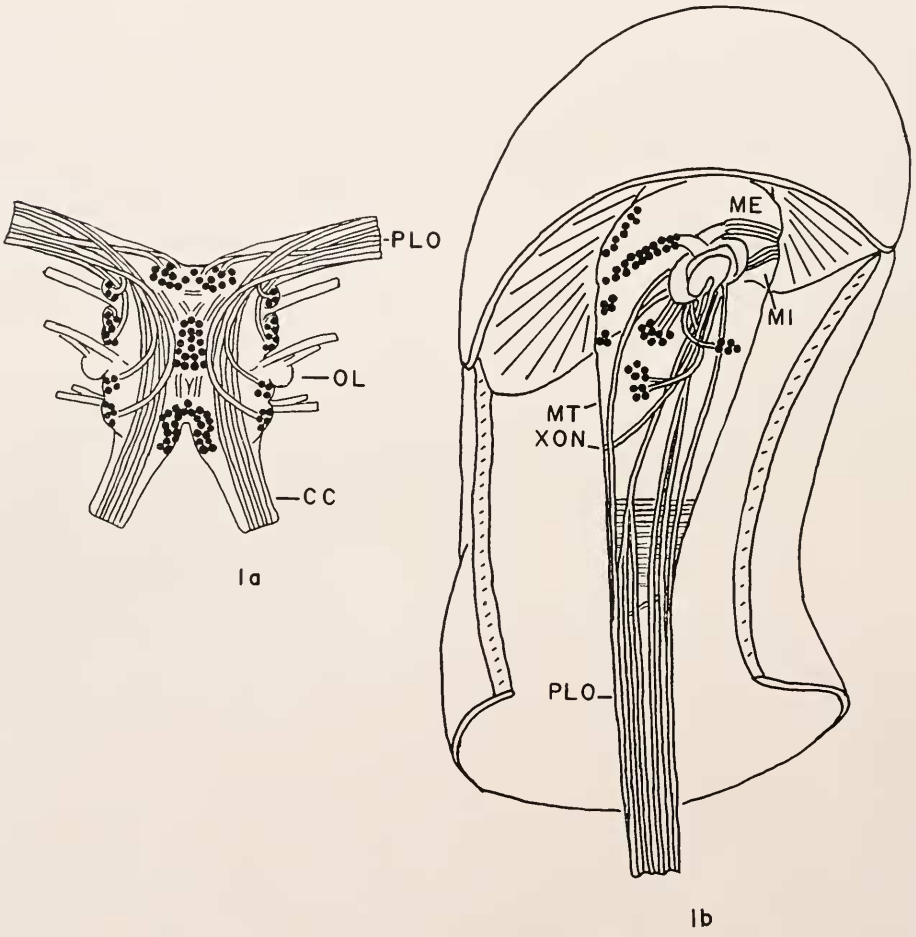


FIGURE 1. Brain (a) and right eyestalk (b) of *Gecarcinus lateralis*, shown in dorsal view when eyestalk is resting in orbit. Circles give location of neurosecretory cell groups. One medial and two lateral groups on the ventral (anterior) face of the brain are not shown. Double lines indicate some of the nerve fiber tracts. Stippled area represents sinus gland. Brain and eyestalk are drawn to the same scale. A considerable portion of the connecting peduncle (PLO) has been omitted. Actual length of adult *Gecarcinus* eyestalk: 0.6–0.7 cm. PLO, peduncle of the optic lobe; OL, olfactory lobe; CC, circumesophageal connective; MT, medulla terminalis; MI, medulla interna; ME, medulla externa; XON, nerve from x-organ.

ganglionic cells accept the stain, these two cell types are then spatially separated by determining in serial sections their relative locations.

Often unstained preparations are best observed in a depression slide against a background of black, white or yellow.

When serial sections are made, tissues are fixed 8 to 12 hours in Helly's, cleared in cedar oil, cut at 6 micra, and stained in chrome-hematoxylin and phloxin, according to Gomori (1941). It has been found that direct immersion of the sections in chrome-hematoxylin without preliminary mordanting in Bouin's results in extraordinarily distinct nerve fibers, whereas after pre-treatment with Bouin's, nerve fibers are relatively indistinct but secretory granules are clearly differentiated.

Observations

Figure 1b shows the right eyestalk of *Gecarcinus lateralis*, as seen in dorsal view with eyestalk in resting position. On casual examination the sinus gland of a freshly-made preparation seems to be innervated by one thick, bluish-white nerve, which is formed at a point proximal to the gland by a branch leading from the ventral portion of the medulla terminalis and one coming from the peduncle of the optic lobe. With application of the several techniques described in the previous section, this nerve is resolved into a number of separate fiber tracts, which intertwine in tortuous fashion as they approach their terminus. Apparent now are many other bluish-white tracts, leading from globules arranged in groups over the surface of the three inner optic ganglia.

The large branch approaching the sinus gland from the proximal ventral portion of the medulla terminalis is the nerve which has been found in crabs by Passano (1951a, 1952a, 1952b) and Bliss (1951, 1952) and in crayfish by Durand (personal communication) to connect the x-organ with the sinus gland. X-organ cells and the nerve which they form are probably identical with the beta cells and the sinus gland nerve of Enami (1951). Bliss and Passano have independently concluded that sinus gland hormone is produced in the x-organ and transported by way of this nerve to the sinus gland. Such a concept is in harmony with that developed for the hypothalamo-hypophyseal system in vertebrates (Scharrer and Scharrer, 1944; Bargmann and Scharrer, 1951; Scharrer, 1952; Palay, 1943, 1945; Smith, 1951), and for the intercerebralis-cardiacum-allatum system in insects (Scharrer and Scharrer, 1944; Scharrer, 1953; Thomsen, 1952).

In Figures 2 and 3 it is shown that, although axons of x-organ cells do form eventually a nerve leading to the sinus gland, the manner in which this is accomplished is quite indirect. The x-organ is composed of two groups of cells, axons of one group forming a tract which descends at once towards the optic lobe peduncle, those of the other group partially circling the medulla terminalis before they head toward the peduncle. Fibers from both tracts now spiral within the peduncle, re-gather in two groups, ascend again to the peduncle, and proceed towards the sinus gland as one large nerve. Evidence for this indirect route has been obtained from glycerine-cleared preparations, both unstained and stained with methylene blue, and from serial sections.

This devious pathway may cause wonder unless it is remembered that the third and fourth optic ganglia are parts of the brain which have, in the course of evolution, been drawn out into the eyestalk. Still pointing towards the center of the

brain, as do axons of many neurosecretory cells within the brain, developing x-organ fibers must turn sharply to reach the sinus gland. Re-orientation may be facilitated by a circling of the optic lobe peduncle. Incidentally there results an increase in the space available for storage of secretory material. Where nerve fibers circle and

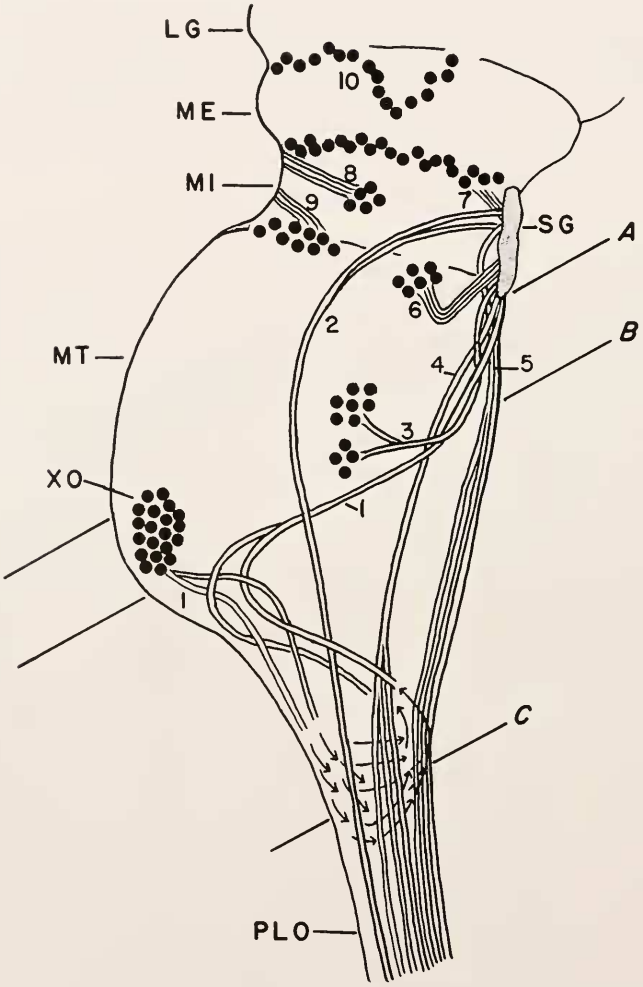


FIGURE 2. The excised right eyestalk ganglia of *Gecarcinus lateralis,* anterior aspect. Circles give location of neurosecretory cell groups. Double lines indicate nerve fiber tracts, which are numbered as in Figure 3. A, B, C designate the three planes of section shown in Figure 3. XO, x-organ; SG, sinus gland; LG, lamina ganglionaris; other abbreviations as in Figure 1.

turn distally towards the sinus gland, secretory material accumulates in such amounts that the axons are almost filled with basophilic granules. This may result from reduced rate of movement in these regions. According to E. Scharrer (personal communication), in vertebrates, likewise, secretory material accumulates at axonal bends and turns.

The original observations that a nerve connects x-organ and sinus gland remain uncontested. The riddle of where the sinus gland nerve runs when, as has been reported often in the literature, it is lost in the medulla terminalis, is solved. This

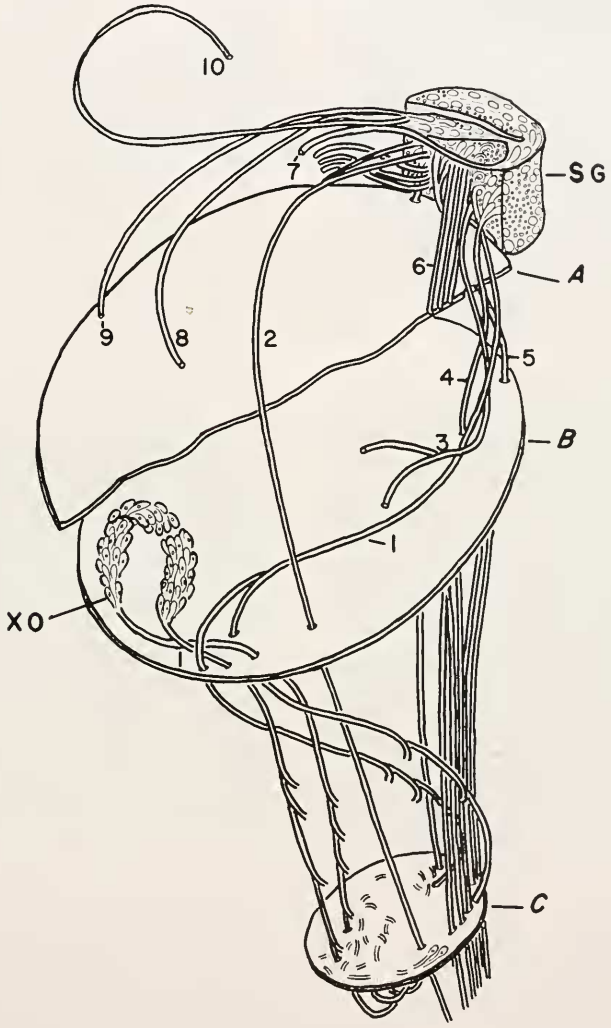
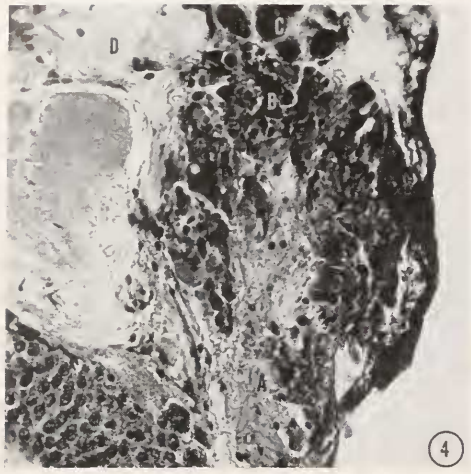
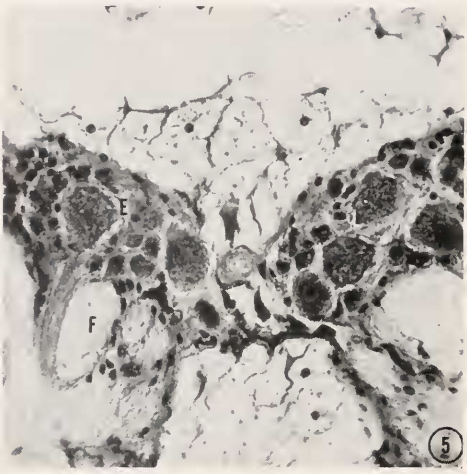


FIGURE 3. Schematic diagram of the x-organ, sinus gland, and fiber tracts of the right eyestalk of *Gecarcinus lateralis*. Fiber tracts and planes of section are designated as in Figure 2. XO, x-organ; SG, sinus gland; 1 (= XON in Figure 1), nerve from x-organ.

nerve has no identity as such before the point where the peduncle-circling fibers converge.

Several groups of bluish-white globules observed proximal to the sinus gland in the living preparation and other groups lying distally (Figs. 1b and 2) are recognizable in chrome-hematoxylin-phloxin stained serial sections as masses of neuro-





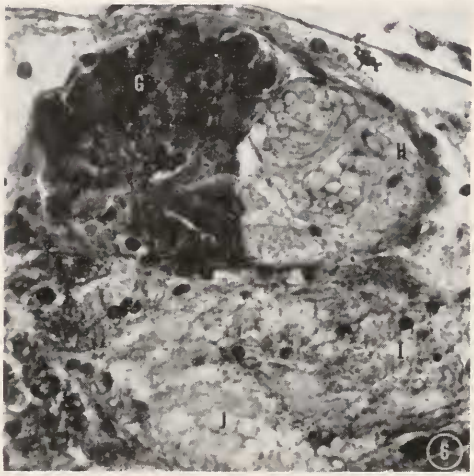


FIGURE 4. Longitudinal section through the sinus gland (right eyestalk of *Gecarcinus lateralis*) in the region where fibers of the x-organ nerve (A) fan out distally to form a sinus gland lobe which has the appearance of an inflorescence. The swollen endings (B) of x-organ axons contain darkly staining secretory material. Distal to the sinus gland are neurosecretory cells (C) and coarse nerve fibers (D) from neurosecretory cells of the medulla interna and medulla externa. Magnification: 200 ×.

FIGURE 5. Two medial frontal groups of neurosecretory cells on the dorsal (posterior) face of the brain of *Gecarcinus lateralis*. In one cell (E) secretory granules fill the axon as well as the cell body. Next to this cell is a large coarse-fibered nerve tract (F) which can be traced in subsequent sections into the optic lobe peduncle. Magnification: 200 ×.

FIGURE 6. Cross section, left eyestalk of *Gecarcinus lateralis*. Included are a small portion of the sinus gland (G), the x-organ nerve fiber tract (H), and fiber tracts (I, J) formed from axons of neurosecretory cells of the brain and medulla terminalis. In x-organ fibers in particular, secretory granules can be seen just inside the fiber membrane. Many granules are visible within the sinus gland. Magnification: 400 ×.

FIGURE 7. A regenerated sinus gland from the right eyestalk of a specimen of *Gecarcinus lateralis* seven and one-half months after both sinus glands had been removed. The regenerated

secretory cells. Coarse lilac-colored axons link cell bodies with the sinus gland. Figure 4 is a longitudinal section showing these coarse axons, the sinus gland, and distal to it large neurosecretory cells. These cells contain concentrically arranged fine granules and irregular inclusions, similar to those described by Hanström (1947) for the cells of the x-organ in Natantia.

Although granules can be seen along an axon for some distance from the secretory cell body, they soon become less numerous or disappear entirely, to appear again in great numbers just before the fiber reaches the sinus gland. The intermediate parts of the fiber contain homogeneous material which stains lilac with chrome-hematoxylin-phloxin. A somewhat analogous situation has been observed in vertebrate hypothalamic-posterior lobe preparations (E. Scharrer, personal communication).

Lying on the surface of the brain (Fig. 1a) are many more neurosecretory cell groups, appearing as collections of bluish globules in the living specimen and as grape-like clusters in serial sections. Figure 5 is a photomicrograph of two medial frontal groups lying on the posterior face of the brain. These neurosecretory cells have the same general characteristics as cells of the insect pars intercerebralis (Scharrer and Scharrer, 1944) and of the vertebrate hypothalamus (Bargmann and Scharrer, 1951; Smith, 1951). They are indistinguishable from neurosecretory cells of the eyestalk of *Gecarcinus* and, like the latter, contain concentrically arranged granular inclusions which stain blue-black with chrome-hematoxylin.

Bluish-white tracts, which appear in serial sections as groups of coarse lilac nerve fibers, run in the living preparation from the globular clusters of the brain into the optic lobe peduncle. Other whitish tracts and, in serial sections, other coarse lilac fibers enter the brain from the circumesophageal connectives and continue out the optic lobe peduncle. Since the thoracic ganglionic mass of *Gecarcinus,* like that of *Sesarma* (Enami, 1951), contains many giant neurosecretory cells, the sinus gland in the eyestalk of a crab appears to be the terminus for axons originating as far away as the thorax. Clearly necessary is a reconsideration of the structure and function of the sinus gland.

Figure 6 shows in cross section the sinus gland and the nerve from the x-organ. Lying just within the membrane of each nerve fiber are granules and granular aggregates, strikingly similar to those found within the cell bodies of these axons and within the sinus gland. In Figure 4 this nerve is seen to be not merely entering but actually forming a portion of the sinus gland. Its fibers, gradually expanding as they terminate to produce the effect of an inflorescence, contain within their bulbous endings acidophilic secretory material and basophilic granules. To the upper left of the sinus gland, axons from neurosecretory cells of the medulla externa approach laterally, to form another section of the sinus gland. Numerous microscopic sections indicate that the sinus gland of *Gecarcinus* is a mass of swollen nerve fiber endings, grouped into lobes according to the fiber tracts from which they arise. This has been represented schematically in Figure 3.

Support for this concept of an organ which previously had been considered glandular in its own right came from regenerated sinus glands. Five weeks after

---

structure is characterized by small size and abnormal position but has essentially normal staining properties. Magnification: 400×. All photomicrographs made from tissues fixed in Helly's, cut at 6 micra, and stained with chrome-hematoxylin-phloxin.

bilateral sinus gland removal the eyestalks of three crabs contained no sign of sinus glands in their normal position. Near the x-organ, just under the connective tissue sheath covering the medulla terminalis of each eyestalk, considerable bluish-white secretory material had accumulated. Fixed and stained with chrome-hematoxylin-phloxin, similar secretory material from a crab, seven and one-half months after bilateral sinus gland removal, resembled histologically (Fig. 7) that found in a normal sinus gland. Fibers from neurosecretory cells of the eyestalk and brain could be traced into this regenerated sinus gland.

Twenty-two days after the x-organ nerve and part of the x-organ itself had been removed from each eyestalk of a crab, one eyestalk retained no sign and the other eyestalk only faint traces of a normal sinus gland. Fibers of remaining x-organ cells and axons from the optic lobe peduncle together had produced on

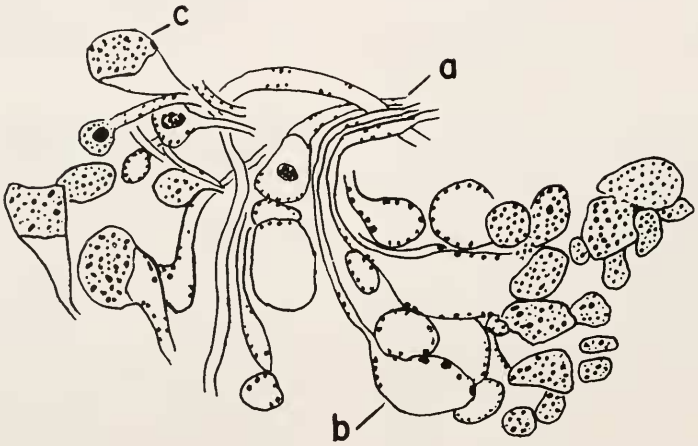


FIGURE 8. A portion of a regenerating sinus gland (right eyestalk of *Gecarcinus lateralis*) which appeared as illustrated after partial removal of both x-organs and x-organ nerves three weeks before had caused degeneration of the normal sinus glands. Secretory granules line the nerve fibers (a) and their swollen endings (b). Many granules have accumulated within masses of acidophilic secretory material (c) which lie at the tips of the bulbous nerve endings.

the medulla terminalis next to the x-organ a regenerating sinus gland, part of which is sketched in Figure 8. Bulbous nerve endings and their acidophilic contents, in which were included basophilic granules, appeared in the same sort of inflorescence as is typical of the normal sinus gland (Fig. 4). Granules lined the nerve fibers and their swollen endings.

Removal of a normal sinus gland seems to cause partial degeneration of neurosecretory cell axons. Upon subsequent regeneration they reach the surface of the ganglion at a point close to the x-organ, where they form a structure in many ways resembling the original sinus gland. Certain respiratory data (Bliss, 1952) suggest that although regenerated sinus glands of *Gecarcinus* continue to release secretory material, the mechanism of release is not normal.

Of considerable interest are the recent reports that regenerated sinus glands are formed in several species of crabs not only after sinus gland removal but also after

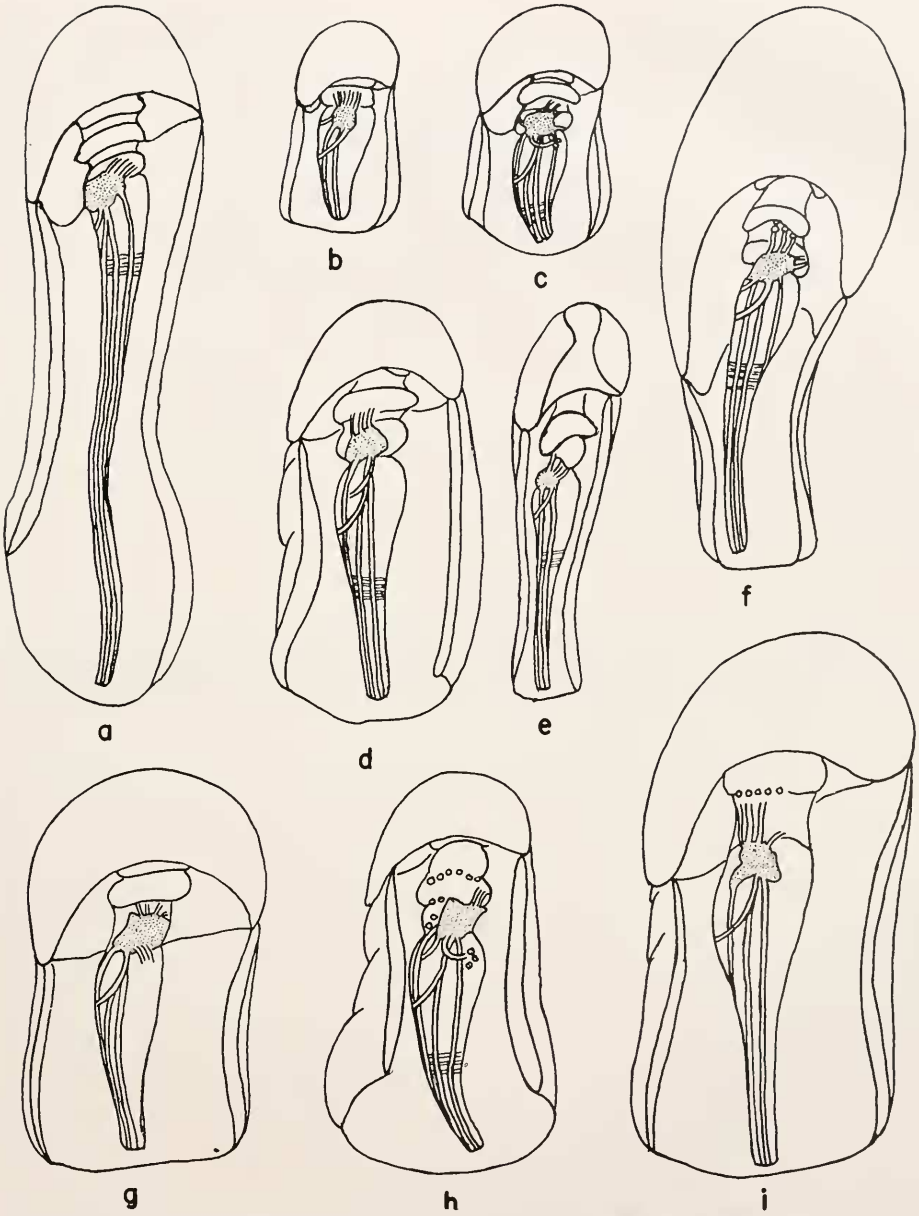


FIGURE 9. Right eyestalks of brachyurans. (a) *Cardiosoma guanhumi;* (b) *Pachygrapsus transversus;* (c) *Sesarma* (*Holometopus*) *ricordi;* (d) *Callinectes ornatus;* (e) *Uca mordax;* (f) *Ocypode albicans;* (g) *Portunus* (*Achelous*) *spinimanus;* (h) *Carcinides maenas;* (i) *Grapsus grapsus.* The eyestalks of *Callinectes exasperatus* are similar to those of *C. ornatus.* Stippled areas represent sinus glands. With one exception (*Uca mordax,* 3½×), all drawings are magnified approximately 2½ times as much as is the *Cardiosoma* drawing. Actual length of adult *Cardiosoma* eyestalk: 2–2½ centimeters.

transection of the nerve from the x-organ (Enami, personal communication; Passano, 1951a, 1952b).

The sinus glands of *Gecarcinus* are receiving centers and storage depots. For some unexplained reason, conceivably related to control of hormone release or perhaps to activation of inactive precursors, secretory products synthesized in the central nervous system are carried by nerve fibers to their swollen endings, the so-called sinus gland, before being released into the hemolymph.

Is this complex synthesizing-transporting-storing-releasing system unique to *Gecarcinus* or does it exist in other Brachyura and in Macrura as well? Observations on eyestalks (Fig. 9) and brain of ten additional species of crabs have revealed the same general pattern of bluish-white globules and nerve tracts and have affirmed the universality of this neurosecretory system in tail-less decapods. The eyestalk and brain morphology of *Cambarus*, to be presented in a later paper, demonstrates the existence of a corresponding system in tailed forms. It is now justifiable to extend the concept first proposed for vertebrates and insects (Scharrer and Scharrer, 1944) to another large group of invertebrates, the decapod Crustacea, and to underscore the possibility that basically similar neurosecretory mechanisms may exist throughout the animal kingdom.

Discussion

Ever since Hanström described the x-organ of the Decapoda, it has been sought and found in many species of Crustacea. Its secretory nature was recognized cytologically but no endocrine function could be attributed to it, particularly since portions of the medulla terminalis containing the x-organ were shown by Hanström to have no chromatophorotropic activity.

The sinus gland of Decapoda has been described by Hanström as a differentiation of the neurilemma (sheath), which had become thick, syncytial, full of radially arranged canals containing secretory material, and innervated by a large, coarse-fibered nerve from the medulla terminalis (Hanström, 1939). Subsequent cytological studies on the sinus gland resulted in confusion concerning its nature and structure. Dethier (1942) described the sinus gland of *Cambarus* as composed of anastomosing rows of cells, yet Pyle (1943) observed no cell boundaries in the sinus gland of *Pinnotheres* or *Homarus* and noted its distal migration during the larval development of *Pinnotheres*. He asked in effect: is the sinus gland a non-cellular storage syncytium?

Smith (1948) observed the bluish-white color of the living sinus gland nerve and the presence of an eosinophilic secretion product in the fixed preparation. A year later, from his experiments on retinal pigment migration following sinus gland removal, he concluded that production of retinal pigment activator in *Hemigrapsus* and *Pachygrapsus* occurs not only in the sinus gland but in many parts of the nervous system as well. For a second time the idea that the sinus gland might be specialized for storage was proposed, Smith suggesting in addition the possibility that the organ might facilitate periodic hormone release. Bowman (1949) found the results of chromatophore experiments in *Hemigrapsus* understandable when the highly active sinus gland was considered a storage-release organ for material produced by chromatophorotropically-active regions of the central nervous system.

The recent observations that eyestalk and x-organ removals, but not sinus gland

removal, induce molting or physiological changes associated with molt (Bliss, 1951, 1952; Frost, Saloum and Kleinholz, 1951; Havel and Kleinholz, 1951; Passano, 1951b, 1952b; Travis, 1951a, 1951b; Welsh, 1951), coupled with microscopic evidence of the presence of secretory material along the nerve connecting x-organ (or beta cells) with the sinus gland (Bliss, 1951, 1952; Durand, personal communication; Enami, 1951; Passano, 1951a, 1952a, 1952b) and along nerves from other neurosecretory cell groups in the eyestalk and brain, have led to the hypothesis presented in this paper, namely, that a large neurosecretory system, involving many parts of the central nervous system, exists in decapod crustaceans, and that the sinus gland is primarily, and perhaps exclusively, a storage and release site for material produced within this neurosecretory system. The initial suggestions made by Pyle, Smith and Bowman have been shown to be justified.

Before concluding, the authors wish to make brief comment on a paper by Enami (1951). After a series of careful histological studies on the eyestalks, brain, and thoracic ganglia, in which the neurosecretory cells of three species of *Sesarma* were mapped, Enami has concluded that the sinus gland and the neurilemma of this organ carry on nuclear secretion. Nothing the present writers have seen has indicated such a process. They suggest that the bulbous nerve endings which make up the sinus gland may have been interpreted by Enami as nuclear capsules and the acidophilic material within those endings as nuclear secretion products.

If the organ which has been named the sinus gland releases but does not synthesize products of secretion, should it still be known by that name? It is an integral part of a diffuse neurosecretory complex, composed of cell bodies, axons, and their swollen endings. It is the portion of this complex which accomplishes the essential processes of storage, possibly of transformation, and of release.

What purposes are served by a diffuse neurosecretory system in contrast to a discrete compact gland? This question can be answered only as physiological data accumulate, but certain possibilities can be suggested. With a large part of the central nervous system occupied by secretory cells and their fiber tracts, it is likely that their specialization for neurosecretion has not eliminated their capacity to act as conductors of nerve impulses. A neurosecretory cell group could then trigger the release of its own secretory material, by conducting impulses to its endings in the storage site. If formed from completely independent groups of neurosecretory cells, the sinus gland might serve as the storage-release center for more than one hormone (see Brown, 1944, 1951; Brown, Sandeen and Webb, 1951; Brown and Hines, 1952; Scharrer, 1953).

Summary

1. The land crab, *Gecarcinus lateralis* (Fréminville), was selected as the principal subject for this study of anatomical relationships existing between neurosecretory centers in the eyestalks and brain of brachyuran Crustacea. Observations were also made on ten other species of crabs.

2. Techniques useful in clarifying crustacean endocrine structures have been described.

3. It has been found that the sinus gland is actually a mass of swollen nerve fiber endings, arranged in the form of an inflorescence and bearing secretory

material. The histological structure of regenerated sinus glands, which appear after sinus gland removal, resembles that of normal sinus glands.

4. Nerve fibers, the endings of which compose the sinus gland, originate in neurosecretory cells of the brain, the eyestalk ganglia, and possibly the thoracic ganglionic mass. X-organ fibers contribute their endings to the sinus gland.

5. Neurosecretory products of the living preparation appear as bluish-white material in the cell bodies, nerve tracts, and sinus gland. When stained with Gomori's chrome-hematoxylin-phloxin, neurosecretory material assumes a homogeneous acidophilic or granular basophilic form.

6. There is developed the concept of a large neurosecretory system involving the brain, cells of the eyestalk ganglia, and perhaps those of the thoracic ganglion, all of which transmit their secretory products to storage-release organs, the so-called sinus glands.

7. The similarities between this system in decapod crustaceans, the hypothalamo-hypophyseal system in vertebrates, and the intercerebralis-cardiacum-allatum system in insects are emphasized. It seems justifiable to extend to the decapod crustaceans the concept first proposed for vertebrates and insects by Scharrer and Scharrer (1944).

8. Recent literature on the histology and physiology of the sinus gland and x-organ is reviewed and interpreted in terms of the hypothesis, proposed in this paper, of a crustacean neurosecretory system.

LITERATURE CITED

Bargmann, W., and E. Scharrer, 1951. The site of origin of the hormones of the posterior pituitary. *Amer. Scien.*, **39**: 255–259.

Bliss, Dorothy E., 1951. Metabolic effects of sinus gland or eyestalk removal in the land crab, *Gecarcinus lateralis*. *Anat. Rec.*, **111**: 502.

Bliss, Dorothy E., 1952. Endocrine control of metabolism in the decapod crustacean, *Gecarcinus lateralis*. Thesis for Ph.D. degree, Radcliffe College.

Bowman, T. E., 1949. Chromatophorotropins in the central nervous organs of the crab, *Hemigrapsus oregonensis*. *Biol. Bull.*, **96**: 238–245.

Brown, F. A., Jr., 1940. The crustacean sinus gland and chromatophore activation. *Physiol. Zool.*, **13**: 343–355.

Brown, F. A., Jr., 1944. Hormones in the Crustacea: their sources and activities. *Quart. Rev. Biol.*, **19**: 32–46, 118–143.

Brown, F. A., Jr., 1951. Regulation of distal retinal pigment cells of the crustacean compound eye. *Anat. Rec.*, **111**: 442.

Brown, F. A., Jr., and Margaret N. Hines, 1952. Modifications in the diurnal pigmentary rhythm of Uca effected by continuous illumination. *Physiol. Zool.*, **25**: 56–70.

Brown, F. A., Jr., Muriel I. Sandeen and H. Marguerite Webb, 1951. Dual control of Palaemonetes red chromatophores. *Anat. Rev.*, **111**: 569.

Dethier, Frances M., 1942. Cytological evidences for function in the sinus gland of the crayfish. Thesis for A.B. degree, Radcliffe College.

Enami, M., 1951. The sources and activities of two chromatophorotropic hormones in crabs of the genus Sesarma. II. Histology of incretory elements. *Biol. Bull.*, **101**: 241–258.

Frost, R., R. Saloum and L. H. Kleinholz, 1951. Effect of sinus gland and of eyestalk removal on rate of oxygen consumption in Astacus. *Anat. Rec.*, **111**: 572.

Gomori, G., 1941. Observations with differential stains on human islets of Langerhans. *Amer. J. Path.*, **17**: 395–406.

Hanström, B., 1939. Hormones in invertebrates. Oxford Univ. Press.

Hanström, B., 1947. The brain, the sense organs, and the incretory organs of the head in the Crustacea Malacostraca. *Kungl. Fysiogr. Sällsk. Handl., N.F.*, **58**: 1–44.

HAVEL, VIRGINIA J., AND L. H. KLEINHOLZ, 1951. Effect of seasonal variation, sinus gland removal, and eyestalk removal on concentration of blood calcium in Astacus. *Anat. Rec.*, **111**: 571.

PALAY, S. L., 1943. Neurosecretion. V. The origin of neurosecretory granules from the nuclei of nerve cells in fishes. *J. Comp. Neur.*, **79**: 247–274.

PALAY, S. L., 1945. Neurosecretion. VII. The preoptico-hypophysial pathway in fishes. *J. Comp. Neur.*, **82**: 129–143.

PASSANO, L. M., 1951a. The x-organ-sinus gland neurosecretory system in crabs. *Anat. Rec.*, **111**: 502.

PASSANO, L. M., 1951b. The x-organ, a neurosecretory gland controlling molting in crabs. *Anat. Rec.*, **111**: 559.

PASSANO, L. M., 1952a. Phase contrast observations on living neurosecretory cells of Sesarma. *Anat. Rec.*, **112**: 460–461.

PASSANO, L. M., 1952b. The x-organ sinus gland complex of brachyuran crustaceans, a neurosecretory molt controlling gland. Thesis for the Ph.D. degree, Yale University.

PYLE, R. W., 1943. The histogenesis and cyclic phenomena of the sinus gland and x-organ in Crustacea. *Biol. Bull.*, **85**: 87–102.

SCHARRER, BERTA, 1952. Neurosecretion. XI. The effects of nerve section on the intercerebralis-cardiacum-allatum system of the insect *Leucophaea maderae*. *Biol. Bull.*, **102**: 261–272.

SCHARRER, BERTA, 1953. Comparative physiology of invertebrate endocrines. *Ann. Rev. Physiol.*, **15**. (In press.)

SCHARRER, BERTA, AND E. SCHARRER, 1944. Neurosecretion. VI. A comparison between the intercerebralis-cardiacum-allatum system of the insects and the hypothalamo-hypophyseal system of the vertebrates. *Biol. Bull.*, **87**: 242–251.

SCHARRER, E., 1952. The storage of neurosecretory material in the neurohypophysis of the rat. *Anat. Rec.*, **112**: 464–465.

SMITH, R. I., 1948. The role of the sinus glands in retinal pigment migration in grapsoid crabs. *Biol. Bull.*, **95**: 169–185.

SMITH, S. W., 1951. The correspondence between hypothalamic neurosecretory material and neurohypophysial material in vertebrates. *Amer. J. Anat.*, **89**: 195–232.

THOMSEN, ELLEN, 1952. Functional significance of the neurosecretory brain cells and the corpus cardiacum in the female blow-fly, *Calliphora erythrocephala* Meig. *J. Exp. Biol.*, **29**: 137–172.

TRAVIS, DOROTHY F., 1951a. Calcium metabolism in the decapod Crustacea. Thesis for Ph.D. degree, Radcliffe College.

TRAVIS, DOROTHY F., 1951b. The control of the sinus glands over certain aspects of calcium metabolism in *Panulirus argus* Latreille. *Anat. Rec.*, **111**: 503.

WELSH, J. H., 1941. The sinus gland and 24-hour cycles of retinal pigment migration in the crayfish. *J. Exp. Zool.*, **86**: 35–49.

WELSH, J. H., 1951. New evidence concerning the source and action of the eyestalk hormone. *Anat. Rec.*, **111**: 442.